

# SOME ASPECTS OF PLANT GEOGRAPHY OF THE NORTHERN HEMISPHERE DURING THE LATE CRETACEOUS AND TERTIARY

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## ABSTRACT

Palynological data emphasize the presence of two distinctive provinces during the Late Cretaceous, one including eastern North America and Europe and a second including the major part of Asia and western North America. The distinction between these two provinces became increasingly blurred during the Paleogene. During the Eocene, the rain forests of both Europe and western North America shared numerous genera, both extinct and extant. The great majority of the latter and most of the closest extant relatives of the former now occur in the Indomalayan region. It is thus clear that much of the present Indomalayan flora represents a relict of a once widespread Northern Hemisphere tropical (s.l.) flora, one that has largely (but not entirely) been eliminated from the New World. Among the possible New World survivors of this boreotropical flora are some of the dry Caribbean genera, which could have been derived from lineages of the dry tropical vegetation of the Gulf Coast Eocene; only a handful of present Neotropical lowland rain forest genera appear to be boreotropical relicts.

Much has been postulated concerning the historical biogeography of the floras of the Northern Hemisphere during the Cretaceous and Tertiary (*e.g.*, Chaney, 1940; Takhtajan, 1969), but many of the suggested migrations and many of the suggested relationships have either turned out to be based on serious misinterpretations of the ages of various fossil floras or on invalid determinations. Paleobotany, particularly that of the angiosperms, has in recent years been undergoing radical changes. The increasing amount of palynological information has contradicted many concepts based on megafossils (particularly foliage; *cf.* Wolfe, 1973), and this has in turn led to reevaluation of some of the fundamental approaches to angiosperm paleobotany (Weber, 1972). In the present report, I will attempt to summarize some of the paleobotanical data that appear to be reliable. From these data, certain tentative conclusions can be drawn concerning ancient floristic relationships; combined with data derived from analyses of the present distribution of some angiosperm groups, hypotheses can be ventured, but I emphasize that many of these hypotheses require confirmation or rejection from future work.

One concept that has particularly influenced some current interpretations of historical biogeography of plants is that of the "Geoflora" (Chaney, 1959). Based originally on the "arcto-tertiary" concept, the geofloral concept was expanded to the "Neotropical Tertiary Geoflora" and the "Madro-Tertiary Geoflora," among others. As has been discussed elsewhere (Wolfe, 1969*a*, 1972), the concept of an "Arcto-Tertiary Geoflora" was based on highly erroneous assumptions regarding the ages of various high latitude plant assemblages. In regard to the "Neotropical Tertiary Geoflora" concept, however, fossil determinations probably have been highly inaccurate. That is, the bulk of the fossil megathermal to mesothermal

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leaf-species determined in western North America in the first part of this century were assigned to genera now exclusively neotropical or were thought to be related to neotropical species in the instances of genera both neotropical and paleotropical (*e.g.*, Chaney & Sanborn, 1933). MacGinitie (1941), however, validly determined a large number of paleotropical elements in the California Eocene. Even more significantly, the only large fructification flora from the Pacific Coast Paleogene has been shown to be overwhelmingly paleotropical (Scott, 1954, and *in* Chandler, 1964: 58), and this calls for a reevaluation of the many leaf imprints of putative neotropical affinities.

One of the basic foundations of this discussion is that the angiosperms are basically of Cretaceous origin and that certainly the major diversification of the angiosperms occurred during the Cretaceous (Doyle, 1969; Wolfe *et al.*, 1975). Thus, the distribution patterns now present in the angiosperm flora are a reflection of events that occurred primarily during the Late Cretaceous and the Cenozoic. These events that directly affected angiosperm distribution fall into two main categories: geographic and climatic. Less controversy surrounds interpretations of the geographic positions of the Northern Hemisphere continents relative to one another than for Southern Hemisphere continents. In regard to paleoclimatic interpretations of the Tertiary, some controversy does exist (Axelrod & Bailey, 1969; Wolfe, 1971), and little paleoclimatic data are available for the Cretaceous.

The Tertiary period is traditionally divided into two major units: the Paleogene and the Neogene (Fig. 1). From the paleobotanical and paleoclimatological record, however, a more meaningful two-fold subdivision of the Tertiary would be by the major climatic deterioration of the Oligocene (ca. 31–32 m.y.; *cf.* Wolfe & Hopkins, 1967; Wolfe, 1971). Prior to that deterioration, Tertiary climates were characterized by high equability (*i.e.*, a low mean annual range of temperature; *cf.* Berry, 1914; MacGinitie, 1941; Traverse, 1955) and, during some periods, high levels of warmth (*i.e.*, high mean annual temperature) to high latitudes (Wolfe, 1971, 1972). The Oligocene deterioration resulted in a major increase in mean annual range of temperature concomitant with a major decrease in mean annual temperature.

The use of the terms “megatherm,” “mesotherm,” and “microtherm” in this discussion follows that of de Candolle (1874) with one modification. While accepting a mean annual temperature of 20°C as separating megatherms from mesotherms, I prefer to place the mesotherm-microtherm boundary at 13°C rather than the 15° proposed by de Candolle. To accept the higher figure would mean that the broadleaved evergreen forest of an area such as Japan would be mesothermal in some areas and microthermal in other areas (*cf.* Wolfe, 1971: fig. 5).

#### REASONING FROM FOSSIL DISTRIBUTIONS

One particular example of how the fossil record can assist in clarifying the problems in historical biogeography is Bombacaceae. Today, the family has its greatest generic and specific diversity in South America. Additionally, some African genera have close relationships to some South American genera, but some African genera also extend into the Indomalayan area. Such a distribution could

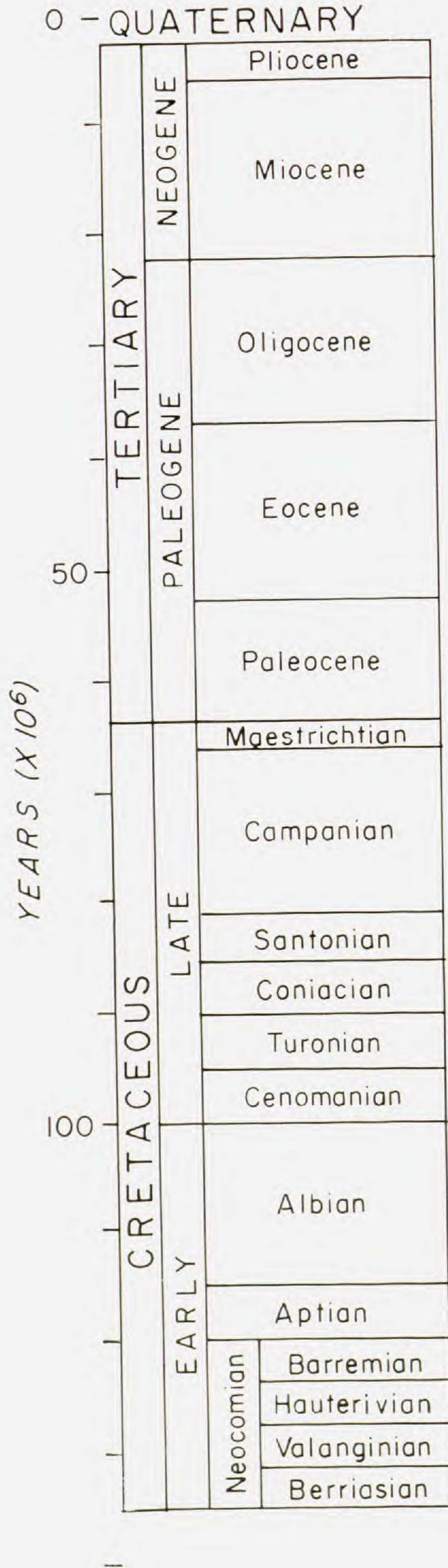
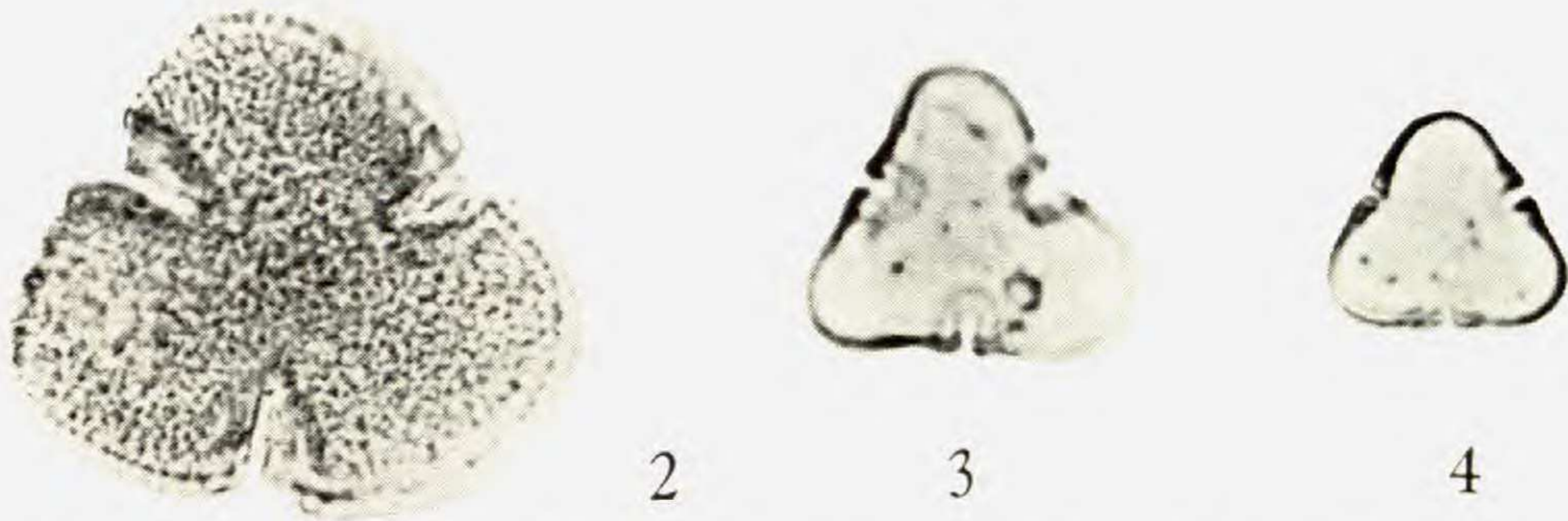


FIGURE 1. Approximate duration of Cretaceous stages and Tertiary epochs (from Wolfe, 1973).



FIGURES 2-4. Pollen from the Upper Cretaceous of the Atlantic Coastal Plain of the eastern United States. All figures  $\times 1,000$ .—2. Bombacaceae, USGS Paleobot. loc. 11223-B, upper part of Navesink Formation (basal Maestrichtian), Atlantic Highlands, New Jersey.—3. USGS Paleobot. loc. 11219-B, lower part of Merchantville Formation (lower Campanian), Oschwald Pit, New Jersey.—4. USGS Paleobot. loc. 11067-B, Cliffwood beds of Magothy Formation (basal Campanian), Cliffwood, New Jersey. The pollen grains illustrated in Figs. 3-4 are closely spaced stratigraphically, whereas the bombacaceous pollen (Fig. 2) is approximately 20 million years younger than the pollen in Fig. 3.

be interpreted to reflect an origin in Gondwanaland, and the Indomalayan genera as reflecting later dispersal from Africa.

In South America, the earliest occurrence of the *Bombax ceiba* type of pollen is in the Paleocene, but, as Germeraad *et al.* (1968: 277) have pointed out, "... the rather sharp lower level of occurrence suggests immigration from elsewhere." The elsewhere was not Africa, because this pollen type first occurs somewhat higher in the section than in South America.

Palynologically, the *Bombax ceiba* type is at a higher grade of specialization (size, sculpture) than other related Bombacaceae (*e.g.*, *Spirotheca* and *Cavanillesia*). Insofar as I am aware, the oldest certain record of Bombacaceae is not in South America but is from the lower Maestrichtian of New Jersey, where pollen highly similar to that of *Cavanillesia* has been found (Fig. 2). Even earlier (in the early Campanian) in this area, pollen that has the same type and location of apertures and shape of grain as in this group of Bombacaceae is encountered (Fig. 3); the sculpturing, however, is simpler than in any extant member of this group of Bombacaceae and the size is also smaller. Yet earlier (in the Santonian and earliest Campanian) is an even smaller and smoother grain (Fig. 4) that also has the basic pattern of shape and pore location of this group of Bombacaceae. In contrast with the sudden entry of advanced types of the family in the South American pollen record, apparently ancestral types occur throughout a 20-million-year span of time in eastern North America. Fuchs (1967) suggested a triphyletic origin of the family, but I think it equally feasible that from eastern North America the family spread into the ancient Aquilapollenites province during the Paleogene, developing a pollen type different from the *Bombax ceiba* type (*i.e.*, the *Durio* type), a relict of which is left in North America (*Huberodendron*). In Asia, the *Durio* type evolved further into the *Adansonia* type, which spread southward into Australasia and westward into Africa and finally reached South America. Thus, the South American Bombacaceae may represent three basically different groups within the family and arrived at three different times: the *Bombax* type in the Paleocene from North America, the *Durio* type at a later date but also from North America, and the *Adansonia* type from Africa.

## THE LATE CRETACEOUS

One of the most striking features of the Northern Hemisphere Late Cretaceous floras is the pronounced floristic difference between the Normapolles and the Aquilapollenites floras. The Normapolles group was dominant in the Late Cretaceous of the eastern United States and Europe. The affinities of this largely extinct group in terms of extant plants has been the subject of much discussion, but increasingly the evidence indicates that several of the so-called amentiferous families, *e.g.*, Juglandaceae, Ulmaceae, and perhaps Betulaceae, were derivatives of the Normapolles stock (Doyle, 1969; Wolfe, 1973). Although the abundance of pollen of the Normapolles group might be an indication of wind pollination, as is the case in the probable survivors of that complex, this applies only to a few of the Normapolles genera in the eastern United States, *viz.*, *Trudopollis*, and *Pseudoplicapollis*. The great majority of Normapolles genera are heavy walled and thus presumably unsuited to wind transport, a suggestion also supported by the rarity of such pollen types in individual samples. There is thus no reason to suspect that the majority of the Normapolles genera were similar in habit or habitat to the few wind-pollinated descendant families.

Despite the fact that Normapolles genera dominated in both Europe and eastern North America, considerable differences are apparent between these two areas. Some Normapolles genera are, of course, common to the two areas, but many are not. Considering the possibility that a pollen genus may well be equivalent to a suprageneric group and that pollen species are typically equivalent to genera, the floristic differences between Europe and eastern North America from at least the Coniacian through the Campanian are significant. There appears to have been little floristic interchange between middle to low latitude regions on either side of the North Atlantic following the Cenomanian until the Maestrichtian.

What the barrier was to interchange is uncertain. The evidence points to the probability that the Normapolles group was largely thermophilic (Wolfe, 1973), and thus the differences between the European and North American members of this group may be largely due to an inability to migrate through the more temperate climates at higher latitudes.

During the later part of the Late Cretaceous, some Normapolles genera are known in western North America and Siberia, but these are few. As noted by many others (*e.g.*, Góczán *et al.*, 1967), this other area constitutes a distinct floristic province characterized by pollen types such as *Aquilapollenites* and *Wodehousia*. Interestingly, Muller (1968) has recorded *Aquilapollenites* from the latest Cretaceous of Borneo, thus placing the Indomalayan region west of Wallace's Line in the *Aquilapollenites* province. In contrast, the latest Cretaceous of Africa and South America have their own pollen flora distinct from that of either Northern Hemisphere provinces.

I do not mean to imply that there was a total lack of floristic interchange between the Normapolles and *Aquilapollenites* provinces. Although extremely rare, *Aquilapollenites* has been encountered in samples from the middle Atlantic States and some Normapolles genera are found in western North America and

Siberia. In general, however, the two regions were effectively isolated floristically. It is not difficult to suggest a reason for these distinctive provinces—their boundaries coincide with the epicontinental seaways that occupied the present sites of the Urals and the High Plains of North America.

Some floristic interchange between the Northern and Southern Hemispheres has been indicated by the occurrence of putatively proteaceous pollen in Northern Hemisphere regions. I can now demonstrate, however, that the so-called *Proteacidites* from eastern North America is in fact a Normapolles derivative that is only convergent with proteaceous pollen, a confirmation of Tschudy's (1971) suggestion. Of course, much podocarpaceous and araucarian pollen is found in the Northern Hemisphere Cretaceous, but such pollen types had the same distribution in the Cenomanian or earlier times.

#### THE PALEOGENE

During the Paleocene and Eocene, the Normapolles group—at least the more basic types—became extinct. Further, various pollen types—both Normapolles and other types of angiosperms—that had been previously restricted to Europe or to eastern North America appeared in the other's subprovince near the Cretaceous/Paleocene boundary. Just as significantly, both megafossil and microfossil data indicate a definite blurring of the distinction between the Normapolles and Aquilapollenites provinces. By the Eocene, the flora of Europe became highly similar to that of western North America, with numerous genera common to both areas.

As opposed to the present floristic kingdoms of the world in which the division in the tropical flora is rather pronounced between neotropical and paleotropical, during the Paleogene the division was more pronounced between the Northern and Southern Hemispheres, that is, a boreotropical kingdom versus an austrotropical kingdom.

The routes by which this boreotropical flora became distributed are not certainly known. One route certainly appears to have been the high latitude Beringian connection between Eurasia and North America (Wolfe, 1972). Fundamentally megathermal families and genera have been recorded from there in profusion during the Eocene, including such basically boreotropical genera as *Magnolia*, *Hypserpa*, *Tinomiscium*, *Meliosma*, *Phytocrene*, and *Mastixia*. A second route could have been via a North Atlantic land connection, which would probably have been at a lower paleolatitude than the Beringian connection (*cf.* McKenna, 1975). Paleobotanical evidence for this route is, however, lacking at the present time.

The floristic affinities of the boreotropical (including both megatherms and mesotherms) flora are very clearly Indomalayan in present distribution. The genera still extant include numerous Menispermaceae and Icacinaceae that are today restricted to this geographic area. Some of the more characteristic extinct genera are members of families such as Mastixiaceae or the tribe Phytocreneae of Icacinaceae, again groups now Indomalayan (Chandler, 1964). Thus, much of the present Indomalayan flora can be thought of as a relict of this Paleogene

boreotropical flora. This also means that even though a particular genus is now restricted to and diverse in Indomalaya, it did not necessarily originate in that region; clearly, the genus could have originated in North America or northern Eurasia, that is, in any of the areas formerly occupied by the boreotropical flora (see below).

Leopold & MacGinitie (1972) indicate that during the Paleogene the floristic affinities of the Rocky Mountain region changed from a dominantly paleotropical to a dominantly neotropical aspect. I suggest that the "neotropical" aspect is not austrotropical; the "neotropical" aspect is rather the result of the evolutionary trends in basically boreotropical groups, that is, the mesothermal boreotropical groups that have survived in North America will naturally become gradually more similar to the survivors in North America than to the survivors of the same groups in Asia.

The geographic extent of the boreotropical flora during the Eocene was variable. During warm intervals, this flora certainly extended to well beyond 50° N. in Europe, that being the most northern occurrence of Eocene plant-bearing deposits on that continent. In western North America, the most northerly Eocene deposits at a paleolatitude of at least 65° N. are clearly boreotropical (Wolfe, 1972). In eastern Asia, the picture is less clear, because the described Eocene assemblages all belong to the late Eocene cool interval; Tanai, however, has reported (oral communication, 1974) that in gross aspects, the as yet undescribed middle Eocene floras from Hokkaido are similar to those of Alaska and Washington. What this indicates, of course, is a similar physiognomy and megathermal climate, but the floristic aspects are still not certainly known.

The Paleogene pollen sequence from Borneo has been interpreted as being similar to the sequences from Nigeria and northern South America, but analysis of the Borneo material does not substantiate such a similarity. As noted previously, the Bornean material from the Upper Cretaceous contains the characteristic northern hemisphere *Aquilapollenites* and, as well, lacks the southern hemisphere true proteaceous pollen. Several of the Bornean pollen types, *e.g.*, *Nypa*, *Anacalosa* type, Rhizophoraceae, and Moraceae, are indeed found in the Paleogene of Africa and South America, but such types are also known in the boreotropical realm during the Paleogene. Some of the more characteristic African and/or South American Paleogene pollen types, *e.g.*, *Ctenolophon*, in fact do not appear in the Bornean succession until the Neogene, but the Bornean Oligocene contains the clearly boreal *Alnus* (Muller, 1966). Such data suggest that in the Paleogene, as in the Cretaceous, the Bornean assemblages represent the southern part of the boreotropical kingdom and that probably, as Reid & Chandler (1933) long ago surmised, the northern shores of Tethys supported a similar flora from Indomalaya northwest to western Europe.

The floristic composition of the Paleogene vegetation of southeastern North America is not well known. Despite the determinations published in an extensive series of papers by E. W. Berry (*e.g.*, 1930), more recent work by Dilcher and his colleagues (*e.g.*, Dilcher & Dolph, 1970; Dilcher, 1973) has demonstrated that most of Berry's determinations were rather fanciful. That extreme caution should be

exercised in accepting any of Berry's determinations is also indicated by the names he applied to foliage that has the cross-hatched petiolules characteristic of Leguminosae and Connaraceae. Such leguminaceous leaflets Berry called *Simaruba*, *Ficus*, *Sapindus*, *Mimusops*, *Banisteria*, *Carapa*, and *Myrcia*.

As yet, no exclusively South American or South American and African genus has been validly determined in the southeastern United States Paleogene. Elements such as *Oreomunnea*, *Engelhardia*, *Paraengelhardtia*, *Populus*, and aff. *Dendropanax*, are clearly Northern Hemisphere in origin. As might be expected, the flora also includes some pantropical elements, for example, *Cochlospermum* and *Memecylon* (Wolfe, unpublished data). The only possible austrotropical element is *Philodendron* (Dilcher, 1973).

During some parts of the Eocene, the southeastern United States had a dry tropical climate. The Claiborne assemblages, for example, have a consistently high representation of entire-margined leaf-species (80% or more), which probably indicates tropical temperatures. The leaves, however, typically lack drip-tips and the majority of the species are microphyllous; additionally, the leaf type associated in many instances with lianas (cordate-based and palmately veined) is uncommon. Therefore, while the climate was tropical, these other foliar characters indicate some deficiency of precipitation.

Whether the dry boreotropical flora of the southeastern United States contributed to the present dry tropical flora of the Caribbean has not been certainly determined. If, however, some of the Antillean region was land during the Eocene, it would appear probable that the flora of such islands would be closely allied to the flora of the southeastern United States. Following the Oligocene deterioration and the elimination of most megatherms from the continental area, some megatherms would surely have survived in the Antillean region. Thus, the present flora of the Antilles may well be derived from two distinct sources: the dry boreotropical Eocene flora and the lineages of austrotropical affinities that adapted to drying conditions in northern South America during the Neogene (Germeraad *et al.*, 1968: 271–272). Clearly, however, further work is needed to establish which source any particular Caribbean lineage had.

During the Paleogene, the boreotropical flora (in at least the humid areas occupied) had a considerably greater uniformity than did the floras of Africa and South America at that time. This interpretation is based, in part, on the many genera—both extinct and extant—that are known from the Paleogene of both Oregon and England (Chandler, 1964: 58–59). Considering the floristic differences between these regions during the Late Cretaceous, the Paleogene similarities almost certainly represent the establishment of direct migrational routes between the two regions. That such a route existed is also strongly indicated by similarities in the earlier Paleogene mammalian faunas of both regions (McKenna, 1975). Interestingly, although McKenna indicates that the direct European-North American mammalian migrations ended at the end of the early Eocene (ca. 49 m.y.), the floristic similarities endured through the early Oligocene (ca. 34 m.y.), which is the age of the Clarno fruit and seed flora (Evernden & James, 1964). In other words, floristic similarities at the generic level were still strong some 15 million years following the last direct migrational path.



## BOREOTROPICAL-AUSTROTROPICAL RELATIONSHIPS

Dispersal of some groups was apparently easy during the Paleogene. An example of one such group is that represented by the olacaceous pollen *Anacolosidites* (this type of pollen characterizes the extant *Anacolosa*, *Cathedra*, and *Ptychopetalum*). According to Germeraad *et al.* (1968), *Anacolosidites* first appears in the Paleocene of Australia, Borneo, Eurasia, and Africa; the only time-lag in the appearance of *Anacolosidites* is in South America, where this pollen type does not appear until the Paleocene-Eocene transition.

As in the case of Bombacaceae cited previously, Menispermaceae (and conceivably Lardizabalaceae) strongly indicate that some floristic interchange occurred between North and South America during the Late Cretaceous and Paleogene, despite the apparent wide geographic separation of the two continents. Representing the same type of long distance dispersal (possibly aided by now-disappeared islands) is section *Lorenzanea* of *Meliosma* and the allied genus *Ophiocaryon*. Certainly *Meliosma* is a boreotropical contribution to the lowland rain forest of South America. Van Buesekom (1972) has strongly suggested that an Eocene species from California is close to the Amazonian *M. sellowii*. Except for the occurrence of *Philodendron* in the Eocene of Tennessee (Dilcher, 1973), I know of no contributions of South American groups to the North American Paleogene flora, but at least a few such contributions are to be expected.

Menispermaceae appear to be a family of boreotropical origin, but one that has successfully invaded the austrotropical region more than once and from more than one direction. In Cocculeae, for example, the North American-Indomalayan *Cocculus* extends into Africa and thence to South America in the form of the monotypic *Ungulipetalum*. All the less advanced genera of this tribe are basically Indomalayan. In contrast, the Anomospermeae and Hyperbaenae, which are endemic to the neotropics, probably represent one or two dispersals from the boreotropical realm via North America; neither tribe has close relatives in Africa or Australia. Tinosporeae are pantropical, but the less advanced members are Indomalayan (Diels, 1910), except for *Calycocarpum* in the southeastern United States; the occurrences of this now mesothermal genus in the Paleogene Clarno flora of Oregon and London Clay flora of England (Chandler, 1964) rather clearly indicate that the Paleogene members were, at least in part, megatherms. One group of genera of Tinosporeae is today African (but one—*Jateorhiza*—is known from the London Clay), and represents one or more dispersals between Eurasia and Africa. Another group of genera is South American, but the only known fossil allied to this group is *Odontocaryoidea* from the Paleogene of Oregon (Scott, 1954, 1956), thus suggesting yet another dispersal of the family from North into South America. Menispermaceae today display no patterns strongly linking the Southern Hemisphere continents, in contrast to the numerous patterns—particularly in the Paleogene—that link the Northern Hemisphere continents. To emphasize this last point, it is highly significant that the same genera of Fibraureae, Tinosporeae, and Cocculeae, are known in both the London Clay and Clarno floras.

The close relationship of the European and African plates during the Paleogene conceivably gave rise to some floristic interchange between the two continents, but

available paleobotanical evidence indicates that such interchange was negligible. The London Clay flora (Chandler, 1964), for example, contains only two dicotyledonous genera of possible African derivation: *Jateorhiza* (Menispermaceae; 2 spp. tropical Africa) and *Oncoba* (Flacourtiaceae; 5 spp. tropical Africa). This possible African element is no larger than the Australasian element, which is composed of *Hibbertia* (Dilleniaceae; 100 spp. Madagascar, New Guinea, Australia, New Caledonia) and *Leucopogon* (Epacridaceae; 150 spp. Malaysia, Australia, New Caledonia). Some London Clay genera that are today both African and Indomalayan may, of course, have originated in Africa and spread to Eurasia during the Paleogene, but there is no available evidence that would indicate such a pattern. One point that deserves emphasis is that, although the African and Eurasian plates could have been adjoining one another, the epicontinental seaways may have been sufficiently wide to have inhibited interchange of land floras—a situation, as was pointed out above, that prevailed in the Cretaceous on the North American plate.

Had there been considerable floristic interchange between Africa and Eurasia during the Late Cretaceous and Paleogene, it would be expected that at least several groups would display disjunctions between the montane flora of Africa and the temperate lowland or montane flora of Eurasia. That is, the floristic disjunctions between the microthermal vegetation of the eastern United States/Upland Mexico and eastern Asia/Himalayas is primarily the result of the participation of such disjunct lineages during the Paleogene in lowland megathermal to mesothermal vegetation throughout the Northern Hemisphere and the subsequent adaptation of such lineages to microthermal climates in both Eurasia and North America (Wolfe, 1969a, 1972). A similar pattern would be expected in microthermal vegetation of Africa and Eurasia if the megathermal vegetation of the two continents could have been readily exchanged. Even more significant is the fact that the generic similarity of the mesothermal vegetation of Africa and Eurasia is extremely low. Genera such as *Meliosma*, *Magnolia*, *Talauma*, *Schima*, *Eurya*, *Liquidambar*, *Persea*, and *Quercus* are common in the mesothermal forests of Asia (Wang, 1961) and are also found in analogous forests in North America. Such genera are basically boreotropical derivatives. No such similarity is found between the mesothermal forests of Africa and Eurasia, and I conclude that this is the result of the lack of contact between the African and Eurasian floras during the Paleogene.

Not until the Neogene does there appear to have been significant floristic interchange between the boreotropical and austrotropical floras. This interchange has been discussed elsewhere (*e.g.*, Lakhanpal, 1970; Raven & Axelrod, 1972) in regard to the paleotropical region. As to which groups entered Africa from Eurasia and which groups had the reverse pattern, the fossil record is, unfortunately, not totally revealing. Neobotanical studies are in this instance of some value. For example, Kanis (1967) suggests that at least some genera of the tribe Ochneae of Ochnaceae entered the Eurasian region from Africa. The monogeneric Ctenolophonaceae, based on their fossil occurrences, almost certainly migrated into the Indomalayan area in the Neogene and have Paleogene occurrences in Africa (Germeraad *et al.*, 1968). Dipterocarpaceae have Paleogene records in the

boreotropical region (Rasky, 1956; Wolfe, 1972), but are unknown in Africa until the Neogene (Lakhanpal, 1970). More information is needed, however, in regard to most now paleotropical groups.

No analogous union of the austrotropical and boreotropical floras occurred in the neotropical region, however, and this phenomenon deserves further consideration.

Following the Oligocene, the boreotropical vegetation became highly restricted areally. Indeed, no megathermal vegetation is known in the Northern Hemisphere during the Neogene in areas that do not now support megathermal vegetation, which is now restricted to areas equatorward of latitude 20° to 25° N. Possibly, megathermal vegetation was even more restricted areally than now; areas such as lowland Taiwan, which is currently occupied by a megathermal rain forest (Li, 1963; Wang, 1961), were occupied by the mesothermal sclerophyllous "oak-laurel" vegetation during the early Miocene (Chaney & Chuang, 1967). I have suggested previously (Wolfe, 1971) that other paleobotanical data can be interpreted in the framework of lower latitudes having warmed during the Neogene.

Some of the boreotropical lineages may have, in fact, become extinct in the northern neotropical region during the Neogene. Langenheim *et al.* (1967), for example, record abundant juglandaceous pollen of the *Engelhardia* type (this includes *Engelhardia*, *Oreomunnea*, and *Alfaroa*) from rocks that represent lagoonal deposits in Chiapas. Langenheim *et al.* (1967) suggested that either the pollen represents an extinct, tropical lowland member of Juglandaceae or extant American genera that produce this pollen type and that are upland today had considerably different tolerances during the latest Oligocene or earliest Miocene than today. A third suggestion to explain this Chiapas occurrence is that, as in eastern Asia, mean annual temperature has increased during the Neogene, that is, *Oreomunnea* and/or *Alfaroa* have not significantly changed their tolerances.

If the third alternative just proposed is accepted as valid, then I suggest that the boreotropical affinities of the montane vegetation of Central America and the austrotropical affinities of the lowland vegetation of the same area become readily understandable. As noted earlier, at latitude 25° N. in Taiwan, a mesothermal climate prevailed during the early Miocene in a now megathermal climatic area. If an analogous situation occurred in North America following the Oligocene deterioration, the potential area of occupation by megathermal vegetation would have been extremely limited to a narrow strip at the southernmost edge of the North American plate. Such a limited area could hardly have supported the diversity previously known in the North American megathermal boreotropical vegetation. On the other hand, the mesothermal boreotropical vegetation would still have occupied considerable areas of the southern United States, perhaps extending even farther north (*cf.* MacGinitie, 1962, for a late Miocene occurrence in Nebraska of mesothermal elements). Thus, the megathermal boreotropical elements would have been limited in number but the mesothermal boreotropical elements still would have been diverse when the North and South American plates merged in the later Neogene. The rising mountains of Central America offered a ready area of occupation for the

boreotropical mesothermal elements, some of which (*Alnus*, *Juglans*) penetrated into South America (Graham, 1973).

In this connection, it is significant that the element in the Rocky Mountain Paleogene floras considered by Leopold & MacGinitie (1972) to be of neotropical affinities is now primarily found in the mesothermal areas of Central America. It is this area to which the North American part of the boreotropical flora is now largely restricted. Had the megathermal part of the American boreotropical flora not become largely extinct (except for some of the possible survivors in the Caribbean region), there would today be less of a distinction between the paleotropical and neotropical floras, that is, there would have been a merging of boreotropical with austrotropical megathermal elements in the New World analogous to the situation in the Old World.

#### THE NEOGENE

The biogeography of many Northern Hemisphere regions during the Neogene (or following the Oligocene deterioration) is much better known than for the Paleogene. This is particularly true for areas poleward from 35°. In areas in which Neogene lineages can be traced back into the Paleogene, generally the lineages had been members of the broadleaved evergreen boreotropical vegetation, or of microthermal vegetation that had been present in upland areas. That is, many of the lineages had adapted at various times during the Paleogene to upland microthermal climates, a phenomenon suggested by Grubov & Federov (*e.g.*, 1964). In other instances, some lineages remained part of dominantly broadleaved evergreen vegetation until the occurrence of the Oligocene climatic deterioration. In yet other instances, lineages gradually adapted from mesothermal to microthermal climates following the deterioration (Wolfe, 1969*a*, 1972).

Although various "floristic elements" have been proposed for species occurring in, for example, the Neogene floras of western North America, the usefulness of recognizing such "elements" is uncertain. The "East Asian" and "East American" elements simply represent those lineages that have become extinct in western North America but whose putatively closest related lineages have survived in these other respective areas. Even if species in such elements are properly placed therein<sup>2</sup>, the only information to be gained is that sometime in the past the extinct lineage and the extant lineage had a common ancestor; no information is gained concerning where or when the divergence occurred. Indeed, it is possible in an instance such as that of *Pterocarya* (s.l.), that an extinct west American lineage could be most closely related to another lineage that has become extinct in eastern North America, where pollen of the *Pterocarya/Cyclocarya* type is known from at least the Oligocene (Traverse, 1955) through the Pliocene (Wolfe, unpublished data). That is, the west American Neogene species of *Pterocarya* could conceivably indicate a strong floristic relationship with eastern North America rather

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<sup>2</sup> Chaney (1959), for example, relates the extinct west American *Quercus simulata* to the extant east Asian *Q.* (*Cyclobalanus*) *myrsinaefolia*, whereas I (1964) consider a more likely relationship to be with (although not ancestral to) the extant west American *Q.* (*Protobalanus*) *chrysolepis*.

than with eastern Asia and the Caucasus, where the sole survivors of the genus occur.

In many respects, the various "floristic elements" currently recognized may represent little more than ecologic convergences. Most of the genera concerned have not been thoroughly studied in the fossil record to determine whether the foliar similarities that supposedly link a fossil species with a particular extant species are of phyletic (and hence floristic) value. In an example discussed later, a species of *Mahonia* from the Miocene of Spain was thought to be related to the west American species of this genus (Amor, 1955). Although in gross morphology some similarities do exist, the fact that the Spanish leaflet is apparently palmately veined (characteristic of the Group Orientales of *Mahonia*) and that the putative relatives in western North America are all pinnately veined (characteristic of the Group Occidentales) indicates that the Spanish occurrence cannot be used to infer a floristic relationship between Spain and western North America during the Miocene.

The salient feature of Neogene microthermal vegetation is, however, that the flora of a given area appears to be largely derived from the preceding flora in that area (MacGinitie, 1962). That is, most lineages of the Neogene at middle to northern latitudes appear to have already been present in the Paleogene in the same area. Little floristic interchange, at least in regard to the ligneous flora, took place between, for example, Eurasia and North America (Wolfe & Leopold, 1967; Wolfe & Tanai, in press). There are, of course, some notable exceptions to this generality, particularly in the instances of Betulaceae and Salicaceae, both families undergoing considerable geographic expansion and specific diversification during the Neogene.

The Beringian area, which functioned as a major floristic pathway between North America and Eurasia during the Paleogene, did not serve as a major pathway for interchange between the broadleaved deciduous forests at middle latitudes of North America and Asia during the Neogene. This is true despite the fact that broadleaved deciduous forest extended in a continuous belt around the Northern Pacific as late as the middle Miocene. Although the middle Miocene flora of the Beringian region contains many species that also occur in Japan and many species that also occur in the Pacific Northwest, few species attained a distribution from the Pacific Northwest to Japan or vice versa (Wolfe & Tanai, in press). Thus, the floristic relationships in the later Cenozoic ligneous plants of the middle and high latitudes of the Northern Hemisphere largely (but not entirely) reflect Paleogene patterns. Van Steenis (1962) validly theorized that the distributional patterns of many now dominantly microthermal genera were bound up with the distributional patterns of mesothermal and megathermal genera.

There is no paleobotanical evidence that the floristic relationships between the dry floras of the Northern Hemisphere region are the result of interchange via low to middle latitude dry corridors. Although I have suggested that during the Eocene the southeastern United States was occupied by a dry tropical forest, it is clear that western Europe was occupied by a wet tropical forest, as was the southwestern United States. That is, during the Eocene there was no dry belt extending from the southwestern United States across into the Mediterranean

region. Indeed, I have shown that some of the so-called "Madro-Tertiary" dry elements were part of humid to mesic forests during the Oligocene and Neogene (Wolfe, 1964, 1969*b*), and the presence of a genus such as *Arbutus* in both western North America and Asia Minor in all probability is a reflection of a more widespread distribution of the genus in humid to mesic broadleaved and coniferous forests of the Paleogene. Axelrod (1966) has, in fact, recorded *Arbutus* from an Eocene flora, for which he inferred a microthermal climate with abundant precipitation well distributed throughout the year.

The berberidaceous *Mahonia* exemplifies in a slightly different manner how a distribution such as that of *Arbutus* could have been developed. One group (Occidentales) of *Mahonia* is centered in western North America and has been considered to be a "Madro-Tertiary" group (Axelrod, 1958), although the earliest record of this type of *Mahonia* is in mesic coniferous forest (Axelrod, 1966; Schorn, 1966). The Group Occidentales has, however, displayed in the Neogene a definite tendency to adapt to and diversify in subhumid to xeric environments (Schorn, 1966). The Group Orientales has an extensive Tertiary record in western North America, and is represented by both mesic and subhumid species; the bulk of this group, however, is now found in the humid to mesic forests of eastern Asia (arriving there by at least the early Miocene; Tanai, 1972). The Orientales, however, also expanded into Europe, where Neogene records include that from Hungary (Andreansky, 1959). Significantly, however, at least one lineage of the Group Orientales adapted to subhumid conditions in the Mediterranean region and has been recorded from the Neogene of Spain (Amor, 1955). *Mahonia*, however, subsequently became extinct in the Mediterranean region.

Yet another and possibly related distribution pattern is that of *Platanus*, which has some mesic species (*e.g.*, in the eastern United States) but could be cited as a floristic link between the dry vegetation of the Near East and southwestern North America. In fact, *Platanus* had a wide distribution in Paleogene (if not Cretaceous) broadleaved evergreen forests and persisted in broadleaved deciduous forests of eastern Asia through the Miocene (Tanai, 1972). In view of such distribution patterns, I suggest that there is no necessity to postulate that the current, rather meager, floristic similarities between dry areas of the Northern Hemisphere reflect a former continuity of dry habitats.

I emphasize, however, that this discussion has involved the ligneous flora. Little is known of the historical biogeography of the major herbaceous groups. A family such as Compositae appeared almost simultaneously on all continents near the Paleogene-Neogene boundary (Muller, 1970), in both tropical and extra-tropical regions. The patterns in such families are reflections of later Cenozoic phenomena, but at this time paleobotany has little to contribute regarding the distributional patterns of many of these advanced families.

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